



Invited Perspectives

Effects of prey characteristics on the feeding behaviors of an apex marine predator, the California moray (*Gymnothorax mordax*)

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ABSTRACT

Moray eels comprise a large radiation of elongate marine predators that are thought to swallow large prey whole but also circumvent gape constraints by manipulating prey into more manageable pieces. Prey manipulation behaviors include shaking, rotation, knotting, and ramming prey against another object to assist in swallowing. Most morays feed on a wide variety of prey that vary in mechanical properties such as stiffness and toughness, which could potentially affect feeding behaviors. There is little diet data informing us of the maximum prey size morays can swallow whole and whether maximum prey size differs between prey types. Our study examines feeding behaviors for the California moray (*Gymnothorax mordax*) in the laboratory. We recorded morays feeding on freshly thawed fish and cephalopods of varying size. We found that prey size had a strong effect on total feeding time and manipulation duration for both fish and cephalopods. While morays were observed using a diversity of prey manipulation behaviors and the durations for each of these behaviors increased with prey size, prey type had no effect on manipulation behaviors employed. Total manipulation duration, however, comprised a greater proportion of total feeding time for fish compared to cephalopods. As relative prey mass (RPM) increased for cephalopods, morays spent a greater proportion of their total feeding time transporting prey. Transport rate was higher for cephalopod prey but the relationship between RPM and transport rate was negative for both prey types. Despite this decrease in transport rate, we attribute the lower total feeding times for larger cephalopod prey compared to fish to behavioral tactics of morays. Morays used the corners of the aquaria to aid in the transport of larger cephalopod prey. We hypothesize that the deformable tissues of cephalopods and the presumably low coefficient of friction of their thawed mantles and tentacles may be difficult for the recurved teeth on the pharyngeal jaws to pierce and grip during transport.

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1. Introduction

Understanding predator–prey size relationships is at the heart of foraging ecology. The role of a predator in a community is often dictated by the maximum size of prey it can consume (Shurin et al., 2006) as well as how often it consumes prey (Huey et al., 2001; Arrington et al., 2002). Maximum prey size is frequently dictated by a predator's gape (Scharf et al., 2000). Animals capable of manipulating prey by removing pieces or specializing on portions of prey can circumvent gape constraints (Jayne et al., 2002). Thus, the size of prey a predator can consume greatly depends on the diversity of the predator's morphological (Cundall and Greene, 2000) or behavioral adaptations for managing prey (Jayne et al., 2002; MacNulty et al., 2014).

Several metrics have been used to quantify prey size in relation to the predator. One common method is dividing prey mass by predator mass, also known as mass ratio or relative prey mass (RPM) (Loop and Bailey, 1972; Greene, 1983; Shine and Thomas, 2005) or 'individual-link predator–prey size relationship' (Nakazawa et al., 2013). Ingestion ratio (IR), where maximum prey circumference is divided by predator head width, has also been an effective metric with which to characterize prey size with respect to the predator. As some predators, such as snakes, possess morphological specializations in the cranium and jaws, studies have found mandible length (ML) to be a better proxy of predator feeding performance than head width (Cundall and Deufel, 2006; Mehta and Burghardt, 2008). These metrics are often applied to individual feeding events to provide a more ecologically informative perspective on predation.

Piscivorous fish predators are an interesting model for predator–prey studies because fish prey vary greatly in shape. A long-term data set on piscivorous marine fishes off the northeast

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US continental shelf was used to examine predator size–prey size relationships to identify general size-based feeding patterns (Scharf et al., 2000). As anticipated, larger individuals of a given species were shown to consume larger prey. However, small prey continued to be included in the diets of larger predators, a result that conflicts with optimal foraging model predictions (Werner and Hall, 1974; Gillen et al., 1981; Harper and Blake, 1988). In both terrestrial and aquatic organisms, the size relationships between predators and their prey have been linked directly to handling time, which incorporates the capture, preparation, and ingestion of prey (Kaspari, 1990). Long handling times during the prey preparation phase may not only be energetically expensive for the predator (Cruz-Neto et al., 2001) but depending on the intricacies of the behavior, may also make the predator vulnerable to its own predators (Dill and Fraser, 1984) and detract from other activities (de Queiroz and de Queiroz, 1987). While optimal foraging models emphasize handling times, the importance of handling or manipulation is thought to vary with feeding habits. For example, piscivores consume prey far less frequently than planktivorous fishes that eat frequently. Since piscivores spend less time feeding overall, longer jaw manipulations or handling times may be of little importance compared to the probability of encountering prey. Therefore, it is not surprising that there are observations of piscivorous predators employing complex jaw manipulation behaviors (Liem, 1979; Grubich et al., 2008) or more time-intensive behaviors involving their entire bodies (Helfman and Clark, 1986; Miller, 1987, 1989) to circumvent gape constraints.

Moray eels (Teleostei: Muraenidae) are enigmatic apex predators recently shown to be influential in coral reef ecosystems (Page et al., 2013). As members of the order Anguilliformes or true eels, morays share an elongate eel body plan and attain rather large body sizes reaching up to 400 cm in total length (Reece and Mehta, 2013). Morays are obligate carnivores consuming a wide variety of prey items including numerous species of fish, cephalopods and crustaceans (Hiatt and Strasburg, 1960; Chave and Randall, 1971; Yukihira et al., 1994).

Similar to other piscivorous fishes, morays are known to consume most prey whole (Young and Winn, 2003; Mehta and Wainwright, 2007; Harrison et al., 2017). A set of morphological and behavioral adaptations enable moray eels to overcome gape limitations when trying to swallow large prey items. A large vertical gape compared with other fishes and expandable folds of skin along the lateral sides of the pharynx have been observed in morays (Mehta, personal observation). Feeding begins by apprehending prey via biting with their oral jaws. Prey is then transported to the esophagus using specialized pharyngeal jaws, which protract from behind the predator's head into the oral cavity to bite prey a second time and transport it to the esophagus (Mehta and Wainwright, 2007, 2008). When faced with prey too large to swallow whole, morays use their wide repertoire of behaviors to manipulate the prey into a more manageable shape, break it apart or remove chunks. Aside from knotting their bodies around prey to gain a firm grip (Miller, 1987; Barley et al., 2015), morays and other anguilliform fishes have been observed rigorously shaking prey in their jaws, rotating it along their primary axis, and ramming it into objects (Helfman and Clark, 1986; Miller, 1987, 1989). Of these behaviors, knotting and rotation of the body are behaviors employed by morays to manipulate prey that exceeds their maximum gape, but not all morays have the ability to form knots with their bodies (Miller, 1989).

Gymnothorax mordax, the California moray, is an elusive predator and the only moray found off the coast of southern California from Pt. Conception down to Baja California, Mexico (Eschmeyer et al., 1983). The present study contributes towards our understanding of the feeding habits of predatory fishes in kelp forest ecosystems by examining the effects of prey size and type on the feeding behavior of the California moray. Preliminary field data

Table 1

Size measurements for California morays, *Gymnothorax mordax*. We anesthetized individuals to measure total length, mass, and horizontal gape width. Horizontal gape was measured as the width between the paired dentary bones in the posterior portion of the mouth.

Individual	Total length (cm)	Mass (kg)	Horizontal gape width (mm)
1	62.0	0.581	34
2	75.0	1.017	37
3	70.0	0.935	38
4	90.5	2.206	52
5	55.0	0.210	22
6	96.3	1.940	40

around Santa Catalina Island suggested that cephalopods and various fish species are a large component of their diet (McCleneghan, 1973; Harrison et al., 2017). While cephalopods and fish are both evasive prey, they represent a wide range of sizes and also vary in mechanical properties, which may potentially affect the prey manipulation behaviors that morays employ as well as the maximum prey sizes morays can swallow. Collagen and elastin fibers, as well as the orientation of circular muscles perpendicular to the longitudinal axis of cephalopods, makes these animals rubbery and stretchy (Bone et al., 1981; Kuo et al., 1991). Fish, on the other hand, have a mineralized endoskeleton and scaled skin that contributes to the overall stiffness of their bodies. Therefore we hypothesize that prey type and prey size will differentially influence the behavioral repertoire, feeding duration, and maximum size of whole prey consumed in the California moray. Specifically, we predict that prey size will increase feeding duration for both fish and cephalopod prey. We also predict that the rigid bodies of fish prey will elicit steeper increases in feeding durations and a greater diversity of prey restraint behaviors.

2. Materials and methods

2.1. Captive husbandry

Six *G. mordax* (size range: 55–96.3 cm total length) were caught in wire mesh eel traps in Two Harbors, Santa Catalina Island, California (33° 23' N, 118° 24' W) and transported to the Long Marine Lab, UCSC, for use in behavioral studies (Table 1) between June 2014 and July 2016. Trapping and collection of *G. mordax* was supported under California Department of Fish and Wildlife Scientific Collecting Permit 11366 to R.S.M., B.A.H. and V.B.B. The size range of specimens examined is well within the range of morays typically trapped around Catalina Island (Mehta, unpublished data). Morays were housed individually in either 25 or 70 gallon salt water (33 ppt) aquaria, depending upon the size of the individual. Each aquarium was outfitted with a 500 gallon Fluval filtration system, an air stone, and a 5 cm diameter opaque plastic tube for refuge. Water temperature was maintained between 20 and 21 °C. Morays were fed a mixed diet of assorted fish and cephalopods weekly. Tanks were cleaned following each feeding. All maintenance and experimental procedures were approved by the Institute of Animal Care and Use Committee at the University of California, Santa Cruz (#1007).

2.2. Feeding trials

To determine the effects of prey size on feeding behavior, two metrics were applied to take into account prey size in relation to the predator: relative prey mass (RPM) and ingestion ratio (IR). In previous studies IR has been defined as the largest diameter of the prey divided by the largest head width of the predator (Loop and Bailey, 1972; Greene, 1983). In morays, horizontal gape distance, mea-

Table 2
Standardized major axis regressions between relative prey mass (RPM) and quantified feeding variables examined in this study (IR = ingestion ratio; TFT = total feeding time, MD = manipulation duration). To fit the assumptions of linear regression, some variables were natural-log transformed (log) prior to analyses.

	R ²	Slope	F-ratio	DF	P-value
Relationship for fish prey					
log RPM × log IR	0.73	0.397	91.22	22	<0.001
log RPM × log TFT	0.65	1.433	8.52	22	<0.001
log RPM × log MD	0.52	1.790	17.56	22	<0.001
log RPM × log MD/TFT	0.22	0.138	354.96	22	0.02
RPM × protractions and retractions	0.593	189.051	2714.59	21	<0.001
log RPM × log transport time	0.62	122.032	168.74	21	<0.001
log RPM × log transport rate*	0.42	-111.041	156.22	21	<0.001
Relationship for cephalopod prey					
log RPM × log IR	0.40	0.817	3.02	44	<0.001
log RPM × log TFT	0.56	1.822	40.26	44	<0.001
log RPM × log MD	0.49	2.287	73.37	44	<0.001
log RPM × log MD/TFT	0.19	0.170	443.56	44	0.002
RPM × protractions and retractions	0.416	114.814	7228.76	44	<0.001
log RPM × log transport time	0.58	112.314	171.53	21	<0.001
log RPM × log transport rate*	0.53	-118.033	162.61	21	<0.001

* transport rate = protractions and retractions/s.

sured as the distance between the dentary bones in the posterior portion of the mouth, is a reasonable indicator of the absolute prey size a moray can swallow whole, as this is the narrowest dimension of the gape when the mouth is fully opened. Thus, as horizontal gape poses the greatest constraint on prey size, IR was calculated as prey depth divided by horizontal gape distance of the predator. RPMs and IRs can thereby range from values close to 0 to greater than 1.0. An RPM or IR greater than 1.0 indicates prey exceeded the mass or the maximum horizontal gape of an individual predator, respectively. To offer morays as many different combinations of RPM and IR as possible for each prey type, cephalopod prey was either long fin squid (*Doryteuthis pealeii*) or California two-spot octopus (*Octopus bimaculoides*) while fish prey varied from small Pacific jack mackerel (*Trachurus symmetricus*) to anchovies (*Engraulis mordax*) to Pacific pompano (*Peprilus simillimus*) and Florida pompano (*Trachinotus carolinus*).

Morays were lightly anesthetized with Tricaine methanesulfonate (MS-222) at the beginning and again at the midpoint of the study to measure total mass and horizontal gape distance to accommodate for the potential growth of the predator throughout the experiment. We found that all measurements remained unchanged and initial recordings can be found in Table 1. Feeding trials were recorded at 30 fps with a Sony A7 digital camera. Once a week, morays were presented with freshly thawed prey (cephalopods or fish) varying in mass and/or diameter while length was kept constant (~200 mm). We chose to feed morays freshly thawed prey items that were constrained in length as part of our experimental design to minimize confounds in our data set. Prey can vary in their level of activity and escape response, which has been shown to have an effect on the feeding behavior of the predator (de Queiroz, 1984). This is especially true with the particular prey categories we were working with – cephalopods and fish, which can have very dynamic escape tactics such as biting, erecting spines, jet-propulsion, and inking. Prey length can also influence prey restraint behavior (Cundall and Greene, 2000) and intraoral transport (Pough and Groves, 1983; Cundall and Deufel, 2006). Thus, any variation in responses to prey in our data set can mainly be attributed to prey size, type, or individual variation in feeding by the predator.

Feeding trials commenced when an individual prey item was immersed in aquaria with 24 cm long forceps. Feeding trials ceased after the prey was entirely consumed. In some trials, manipulation resulted in morays removing pieces from prey and/or unfinished meals. Trials where meals were not completely consumed were only analyzed using a logistic model regression (see below). Most variables measured were time dependent, and feeding trials where

the meal was not finished were undoubtedly shorter and fewer behaviors were deployed. Feeding trials lasted from July 14th 2014 through August 2016.

2.3. Analyses of feeding trials

Feeding trials were analyzed frame by frame in the video editing software, Final Cut Pro X (Apple Inc., Cupertino, CA, USA). Each video was analyzed for: (i) total feeding time (s) – the duration from when the moray contacted prey with its oral jaws until the prey disappeared into the throat; (ii) manipulation duration (s) – the duration a moray spent in a prey manipulation behavior during a single feeding trial; for example, if a moray knotted multiple times during a trial, each knotting event was quantified and then all knotting events were summed to produce a knotting duration for that trial; (iii) total manipulation duration (s) – the total duration spent manipulating prey. For total manipulation duration, the durations for all behaviors were summed. When morays were not manipulating prey, time was spent transporting prey into the oral cavity (swallowing). Therefore, (iv) transport time (s) was calculated by subtracting total manipulation duration from total feeding time. During transport time, we could observe and therefore quantify the number of pharyngeal protraction and retraction events during transport. Obtaining the number of pharyngeal protraction and retraction events and transport time enabled us to calculate another variable, (v) transport rate (protractions and retractions/s).

The definitions for behaviors used in the current study were adopted from Helfman and Clark (1986) and Miller (1987, 1989) and are: *body rotation* – movement along the eel's longitudinal axis; *shaking* – rigorous horizontal (left-to-right) movements of the head; *knotting* – formation of loops in a figure eight fashion which tighten upward from the tail to the head; and *ramming* – use of force against another object or the substrate to facilitate prey transport/swallowing. Each of these behaviors was often repeated multiple times.

We used a *t*-test and a Levene's test to determine whether the means and variances between the two prey size metrics, RPM and IR, differed for both fish and cephalopods. We used a mixed model least-squares regression non-random effects test to detect whether individual morays differed in their total feeding time and total manipulation duration, the two continuous variables that were our measure of response to increasing prey size. Standardized major axis (SMA) regression analyses were run on natural log-transformed (log) data to examine the relationship between IR, RPM, total feeding time, and manipulation duration for

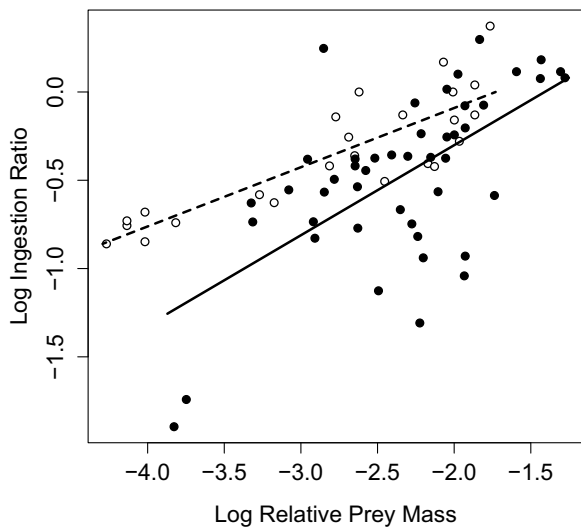


Fig. 1. The relationship between two metrics used to describe prey size in relation to the predator, the California moray, *Gymnothorax mordax*. Variables were natural-log transformed (log) prior to regressions. Separate linear regression lines are shown for fish (dashed) and cephalopods (solid). Open circles represent fish prey while filled circles represent cephalopod prey offered in feeding trials.

cephalopods and fish. After the size metric exhibiting the strongest relationship with total feeding time for both prey types was determined, SMA regressions were carried out to examine the effects of size on (i) total manipulation duration; (ii) the proportion of total feeding time morays spent manipulating prey by knotting, shaking, ramming, and rotational feeding; (iii) transport time; (iv) the number of protractions and retractions during transport; and (v) transport rate. The number of protractions and retractions was the only variable that was not log-transformed. We then tested whether the slopes of these regression lines differed between prey types as prey size increased. If slopes were similar, we tested whether RMA regression lines for prey type were equivalent in elevation using the Wald statistic (Warton et al., 2006).

To determine whether *G. mordax* apportioned manipulation durations differently across prey types, a principal components analysis (PCA) was run on the log-transformed duration of each manipulation behavior. Since there were four manipulation behaviors, the PCA yielded four principal components. The first principal component was one on which all four behavior durations loaded positively and strongly, indicating that this PC captured the effects of prey size on manipulation durations (Jolicoeur, 1963). The remaining PCs were thus interpreted to capture size-independent variation in manipulation durations. A MANOVA was then run using scores from all four principal components as dependent variables and prey type as the independent variable. An additional MANOVA was run using only scores from PCs 2–4, the size-free axes, to investigate whether *G. mordax* employed different manipulation behavior durations across prey types when the effects of prey size were removed.

Logistic regression was used to assess whether prey characteristics (size and type) could be used to predict if *G. mordax* would consume prey whole. Here, RPM, IR, prey type, and interactions between these variables were used as predictors in a binary logistic model to predict the odds of morays removing pieces from prey. Estimation involved a “complete” method, whereby all variables were entered in the regression in a single step. Because logistic regression does not make many of the key assumptions that linear regression or other linear methods do, RPM and IR data were not log-transformed for this analysis. All statistical tests were performed in R (R Development Core Team, 2014).

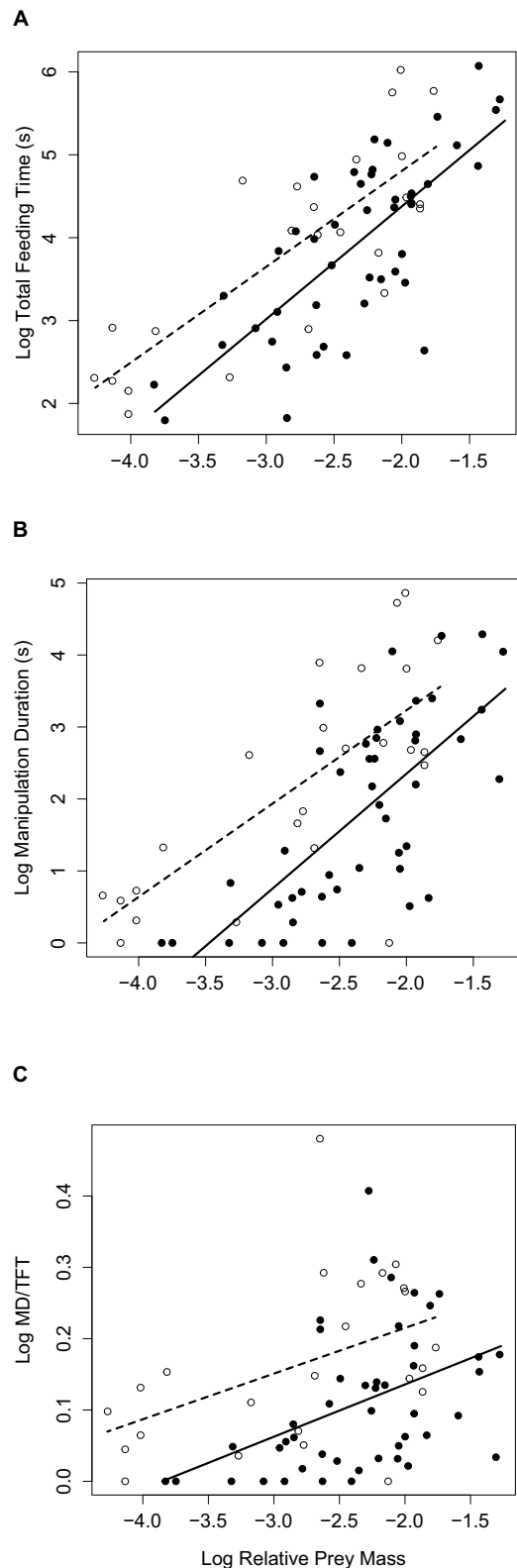


Fig. 2. Relationships between relative prey mass (RPM) and (A) total feeding time (TFT), (B) manipulation duration (MD), and (C) MD as a proportion of TFT. Each variable was natural log-transformed (log) prior to regression analyses. Each data point represents a feeding trial. Open circles are feeding trials with fish while filled circles are trials with cephalopods. As size increased for both prey types, TFT, MD, and the ratio between the two significantly increased (see Table 2 for more details).

Table 3
Slope tests and intercept tests for standardized major axis regressions between relative prey mass (RPM) and quantified feeding variables examined in this study (IR = ingestion ratio; MD = manipulation duration; Prot-Ret = protractions and retractions; TFT = total feeding time). Significant values are in bold.

Slope tests	Likelihood ratio	p-value	Fish slope (95% CI)	Squid slope (95% CI)
log TFT vs log RPM	2.151924	0.142	1.43 (1.10–1.85)	1.82 (1.49–2.22)
log MD vs log RPM	1.728273	0.188	1.79 (1.32–2.42)	2.28 (1.84–2.83)
log MD/TFT vs log RPM	0.7717458	0.379	0.13 (0.09–0.20)	0.16 (0.12–0.22)
# of Prot-Ret vs RPM	3.556	0.064	0.78 (–2.72–4.37)	–3.36 (–7.06–0.63)
log transport time vs. log RPM	2.572	0.108	1.382 (1.063–1.797)	1.809 (1.470–2.227)
log transport rate* vs. log RPM	3.198	0.073	–0.581 (–0.395 to –0.856)	–0.891 (–0.680 to –1.168)
Intercept tests	Wald statistic	p-value	Fish intercept (95% CI)	Squid intercept (95% CI)
log TFT vs log RPM	11.38656	<0.0001	8.51 (7.67–9.36)	7.79 (7.13–8.45)
log MD vs log RPM	18.46637	<0.0001	8.06 (6.86–9.25)	6.71 (5.79–7.63)
log MD/TFT vs log RPM	14.92919	<0.001	0.604 (0.48–0.71)	0.479 (0.39–0.56)
# of Prot-Ret vs RPM	5.311279	0.021	0.83 (–3.82–5.49)	–4.46 (–9.36–0.43)
log transport time vs. log RPM	8.246	0.0040	8.163 (7.31–9.01)	7.54 (6.87–8.21)
log transport rate* vs. log RPM	5.521	0.018	–3.236 (–3.802 to –2.671)	–2.868 (–3.303 to –2.434)

* Transport rate = Prot-Ret/s.

Table 4
PCA loadings are correlations between each of the original behavioral variables and each PC axis. The percent variance for which each PC accounted is included in the column headings. Bolded loadings represent relatively strong correlations ($|value| > 0.4$).

Natural-log transformed durations	PC1 (61.90%)	PC2 (18.89%)	PC3 (12.00%)	PC4 (7.20%)
Knotting	0.769	–0.497	0.306	0.263
Shaking	0.674	0.702	0.109	0.200
Rotation	0.800	–0.125	–0.585	0.046
Ramming	0.889	0.009	0.179	–0.420

3. Results

3.1. Prey size

We recorded over 97 trials of *G. mordax* feeding on freshly thawed prey. Of these trials, 68 feeding events ($N = 46$ cephalopods, $N = 22$ fish) resulted in morays consuming entire prey whole. In the remaining trials, morays dismembered prey and consumed it in chunks. While only trials where prey were consumed whole were examined for the effects of prey size and type on feeding behavior, all trials were used in our logistic regression model to assess which prey characteristics best predicted the consumption of whole prey.

For the two prey types in our data set, the relationship between RPM and IR was strong and positive for fish ($R^2 = 0.73$; $F_{22} = 91.22$; $p < 0.001$) and weakly positive for cephalopods ($R^2 = 0.40$; $F_{44} = 3.02$; $p < 0.001$; Table 2 and Fig. 1). A t -test and Levene's test indicated that the mean and variance for relative prey mass was significantly different between cephalopods (0.04–0.27) and fish (0.01–0.15) trials ($t = 396.2$; $p = 0.01$) while a two-tailed t -test did not detect any differences between the range of ingestion ratios for cephalopods (0.32–1.3) or fish (0.4–1.45; $t = 0.22$; $p = 0.823$). Therefore, the range of relative prey masses differed between cephalopods and fish in our data set while ingestion ratios for prey items were similar and the lengths of both prey types were kept constant.

According to a mixed model least-squares regression non-random effects test, there were no significant differences between an individual's responses to prey size with respect to total feeding time for either prey type (fish: $F_5 = 0.719$, $p = 0.505$; cephalopods: $F_5 = 0.103$, $p = 0.978$) or manipulation duration (fish: $F_5 = 0.937$, $p = 0.415$; cephalopods: $F_5 = 1.108$, $p = 0.423$). Therefore, feeding trials for individuals were pooled for subsequent analyses.

When examining cephalopods and fish trials we found a strong positive relationship between log RPM and log total feeding time (fish: $R^2 = 0.65$; $F = 8.52$; $p < 0.001$; cephalopods: $R^2 = 0.56$; $F = 34.8$; $p < 0.001$; Fig. 2A). Trials with fish exhibited a strong relationship between log IR and log total feeding time ($R^2 = 0.89$; $F = 195.01$; $p < 0.0001$), while cephalopod trials exhibited a weaker relationship between log IR and log total feeding time ($R^2 = 0.40$; $F = 39.06$; p

< 0.03 ; Table 2). Therefore, since RPM accounted for variation in total feeding time better than IR for both prey types, RPM was selected to examine the effects of prey size and type on prey manipulation behavior.

3.2. Manipulation behaviors

Most feeding trials analyzed required some form of prey manipulation prior to swallowing. *G. mordax* exhibited most manipulation behaviors reported for morays: shaking, knotting, rotation, and ramming. In many of these trials, irrespective of prey type, multiple behaviors were employed (see supplementary Videos S1–S3 in the online version at DOI: [10.1016/j.zool.2017.03.002](https://doi.org/10.1016/j.zool.2017.03.002)). There were no significant differences between individuals in log total manipulation duration as a function of log RPM for either prey type (cephalopods: $F_2 = 2.340$, $p = 0.06$; fish: $F_2 = 1.095$, $p = 0.14$) and data were pooled for the following analyses. We detected a significant relationship between log RPM and log manipulation duration for both cephalopods ($R^2 = 0.49$; $F_1, 44 = 73.37$, $p < 0.001$) and fish prey ($R^2 = 0.52$, $F_1, 22 = 17.56$, $p < 0.001$; Fig. 2B and Table 2). When examining the relationship between log RPM and the log of the ratio of total manipulation duration to total feeding time, we found a positive but weak relationship for both prey types (fish: $R^2 = 0.22$, $F_1, 18 = 11.71$, $p < 0.002$; cephalopods: $R^2 = 0.19$, $F_1, 18 = 443.56$, $p < 0.002$; Fig. 2C). A likelihood ratio test did not detect a difference in slopes between any of the SMA regression lines for fish and squid in total feeding time, manipulation duration, and the ratio of manipulation duration and total feeding time (Table 3). We then tested whether the elevation of the SMA regression lines differed between fish and cephalopods for each of the dependent variables by testing for equal mean residual scores across groups using the Wald statistic. We found that the SMA intercepts were significantly different between fish and cephalopods for all three dependent variables with the SMA regression lines for fish consistently having the higher elevation over cephalopods (Table 3). An assumption of this test is that the different groups all have the same slope, which we have shown.

The PCA yielded four principal components (Table 4). The first principal component (PC1) accounted for 62% of the variance, and all manipulation durations loaded strongly and positively on PC1 (Table 4 and Fig. 3). PC1 was the only axis that showed correlation with RPM (ordinary least-squares regression: $R^2 = 0.32$, F -ratio: 33.94; $p < 0.001$; Fig. 3) revealing that individual manipulation behaviors varied in duration according to prey size. On each of the subsequent PCs, one or two behaviors loaded strongly (i.e., absolute value of the loading > 0.4). On PC2, knotting duration loaded strongly and negatively, while shaking duration loaded strongly and positively (Fig. 3). Each of the subsequent PCs had strong loadings for a single behavioral duration (rotation duration for PC3 and ramming duration for PC4; Fig. 3). The MANOVA, which was used to analyze scores from all PCs, did not detect any differences in mean PC scores between fish and cephalopod trials (two-sample Hotelling's T -square: 1.563, p -value: 0.831). Additionally, the MANOVA using scores from PCs 2–4 (the size-free axes) only similarly showed no difference in mean PC scores between the prey types (two-sample Hotelling's T -square: 0.961, p -value: 0.451).

3.3. Effects of prey type on transport

A general linear model was used to test for significance of interactions between prey type size metric, and protractions and retractions. There was no interaction between prey type and RPM (F -ratio = 3.556; $p = 0.064$; Fig. 4A). Since the slopes for protraction and retraction versus RPM for each prey type did not significantly differ, we tested for the elevation between the RMA regression lines for prey type. The Wald statistic showed a significant difference in elevation between the regression lines for cephalopods and fish with fish having the higher regression line ($p = 0.021$; Table 3). There was a strong positive relationship between log RPM and transport time (fish: $R^2 = 0.62$, $p < 0.001$; cephalopods: $R^2 = 0.58$, $p < 0.001$; Fig. 4B). We also found that the slopes for log RPM and log transport time did not differ between prey types, and the Wald statistic showed significant differences in elevation between fish and cephalopods ($p = 0.004$; Fig. 4B and Table 3). The relationship between log RPM and log rate of transport was negative for both fish ($R^2 = 0.42$, $p < 0.001$) and cephalopods ($R^2 = 0.53$, $p < 0.001$; Fig. 4C). The slopes of the RMA regression lines for log of RPM and log rate of transport between fish and cephalopods did not differ. Again, the Wald statistic showed a significant difference in elevation between the regression lines for fish and cephalopods ($p = 0.018$; Table 3) with cephalopods, this time, exhibiting longer transport times.

3.4. Maximum size of prey swallowed whole

We used logistic regression to determine whether prey characteristics could predict at which point morays would stop consuming prey whole and transition to consuming chunks of prey. Logistic regression correctly classified whether prey in trials ($N = 85$) were consumed whole with 85.9% accuracy. The overall model had a chi-square value of 185.17 ($p < 0.001$) with R^2 of 0.755. The sensitivity was 0.912, the specificity was 0.714, and the area under the ROC curve was 0.923. In this model, the interaction between prey RPM, IR and prey type was identified as the strongest predictor (Z -value: -2.011 , $p = 0.04$), and the interaction between RPM and prey type also provided valuable information (Z -value: 1.925, $p = 0.05$), indicating that fish prey with higher IRs (> 1) were typically consumed in pieces (Fig. 5). All other predictors did not achieve statistical significance (i.e. all p -values > 0.05).

In the present data set, maximum prey sizes consumed whole exceeded IRs of 1.0 for both cephalopods (IR = 1.2) and fish (IR = 1.2). Trials that exceeded IRs of 1.0 (log of IR is equal to zero) did not

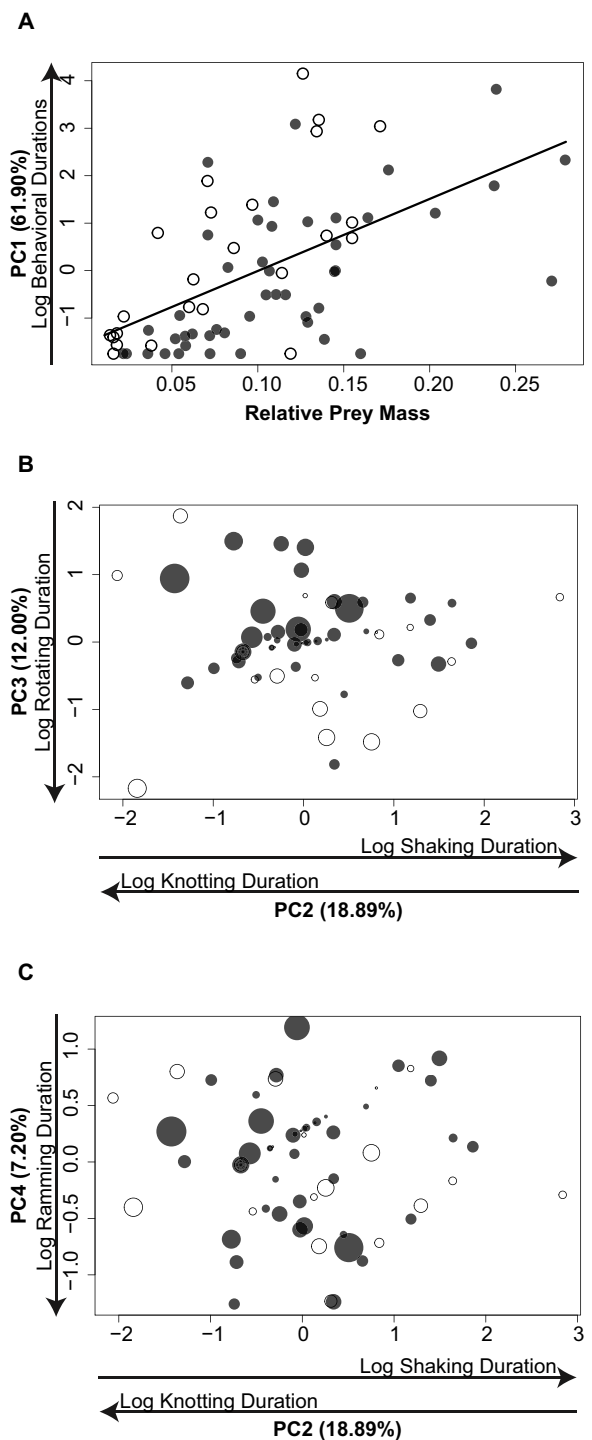


Fig. 3. The distribution of prey manipulation behaviors across feeding trials. (A) Ordinary least-squares regression shows correlation between relative prey mass (RPM) and PC1 - natural log-transformed (log) behavioral durations ($R^2 = 0.32$; F -ratio = 33.94; $p < 0.001$). PC1 was the size axis. All behavioral durations for the four different manipulation behaviors loaded strongly on PC1, which accounted for 59.14% of the variation in the behavioral PCA. (B) Long durations of knotting and shaking occupied opposite ends of the duration continuum (PC2) revealing that morays tended to employ one of these strategies. Knotting or shaking could be observed with rotational feeding and (C) ramming. A MANOVA using scores from only PCs 2–4 showed no difference in mean PC scores between prey types. Each data point represents a feeding trial. Open circles are feeding trials with fish while filled circles are trials with cephalopods. The size of the circles is proportional to prey size.

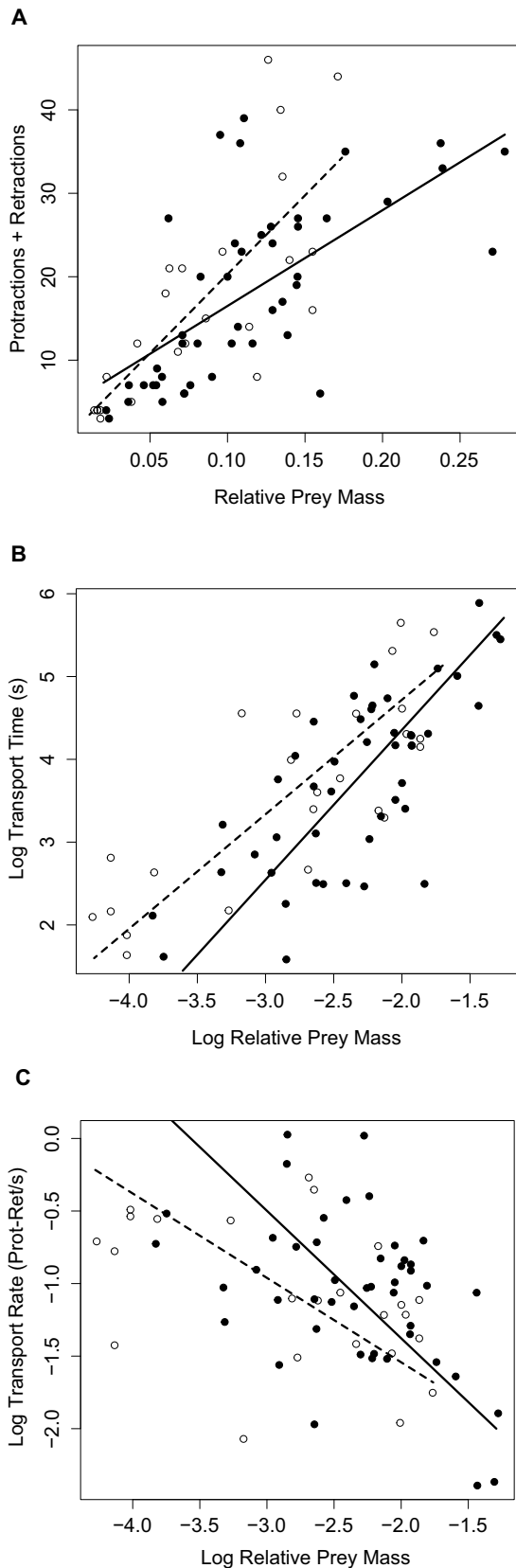


Fig. 4. The relationship between relative prey mass (RPM), prey type, and transport. (A) The relationship between protraction and retraction events and RPM was strong for both fish and cephalopod prey. (B) The relationship between log RPM and log transport time was positive for both prey types. (C) The relationship between log RPM and log transport rate (protractions and retractions/s) was negative for both prey types. Filled symbols depict cephalopod trials, while open symbols depict fish. Dashed lines represent SMA regression lines for fish while solid lines are for cephalopod prey.

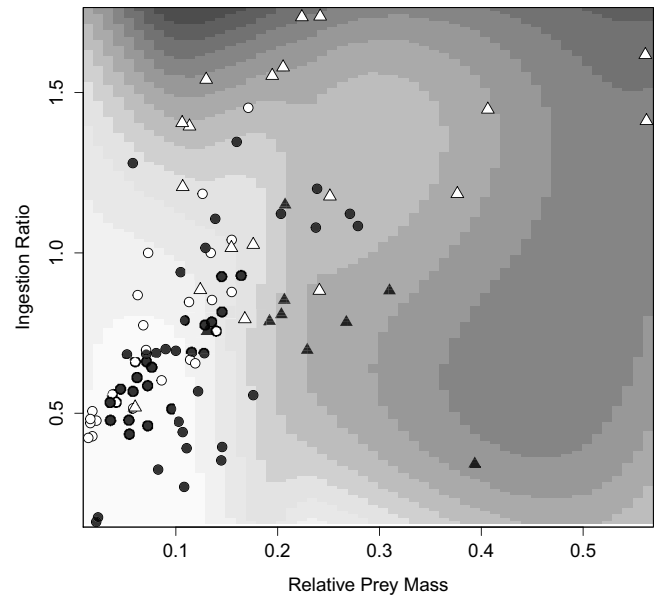


Fig. 5. The probability of morays removing pieces of prey in all feeding trials ($N = 85$) as predicted by logistic regression. Circles correspond to trials where prey was consumed whole; triangles represent trials in which piece removal occurred. Filled symbols depict cephalopod trials, while open symbols depict fish. The shaded contours within the scatterplot area represent the probability of piece removal of prey (ranging from 0 to 1), as predicted by the fitted logistic regression model. Lighter shading corresponds to regions of higher probability of consuming prey whole, while dark shadings represent regions of high piece removal probability.

correspond to the maximum RPM for our data set for cephalopods (RPM = 0.27) or fish (RPM = 0.15; Fig. 1).

4. Discussion

4.1. Metrics of prey size

The two metrics adopted for evaluating prey size in relation to the predator, RPM and IR, were positively correlated for both cephalopods and fish. The stronger positive relationship between RPM and IR for fish ($R^2 = 0.73$) compared to that of cephalopods ($R^2 = 0.40$) suggests that as the fish prey offered increased in size, both mass and width also increased appreciably (Fig. 1), while this relationship was less pronounced for cephalopods. This is further supported by the fact that, using either prey size metric, there was a substantial increase in total feeding time with fish prey whereas only RPM was a good predictor of total feeding time for cephalopod prey. This result was achieved by feeding morays different species of fish that vary in body shape.

While length of prey was held constant, RPM for cephalopods that were consumed whole was nearly double the range of RPMs for fish, while the range of IRs was equivalent for both prey types. Combined, fish and cephalopod prey provided a relatively wide range of size possibilities for our captive morays (RPMs: 0.01–0.27). Thus, individual morays fed on prey that varied from 1% to 27% of their own body mass.

While the majority of our behavioral analyses focused on morays feeding on prey that were consumed in their entirety, our logistic regression analyses showed that IR was the best predictor of whether fish prey would be consumed whole or in chunks. In our prey range, manipulation behaviors were used to remove pieces from fish with high IR values that exceeded the maximum horizontal gape of our predators. The majority of these feeding trials with high IR fish prey resulted in morays leaving their meals unfinished. We observed this to an even greater extent with cephalopod

prey. If the moray could not transport cephalopod prey whole, it tended to abandon the prey.

4.2. Effects of prey size

As we had hypothesized, total feeding time, manipulation duration, and the ratio of manipulation behavior to total feeding time for *G. morax* were significantly influenced by prey size (Fig. 2A–C). The larger the prey item offered, the longer the morays would take to manipulate and swallow the meal whole. With increasing RPM, the increase in total feeding time and manipulation duration was greater for fish compared to cephalopods as revealed by the RMA regression lines and the Wald statistic, which we used to test for equal elevation of the regression lines.

We found a strong positive relationship between RPM and the number of protractions and retractions for both squid and fish but the slope was much steeper for fish indicating that more transport cycles were required as fish size increased. We also found that transport time was greater for fish compared to cephalopods. Most interesting was the negative relationship between log of relative prey mass and transport rate (Fig. 4C). Even more surprising was that cephalopod prey elicited higher transport rates in moray predators compared to fish prey. The majority of the feeding variables measured in our present study were much greater for fish prey compared to cephalopod prey. However, transport rate revealed that cephalopods present more of a challenge for swallowing, especially at smaller relative prey mass. When morays were offered smaller cephalopod prey, we observed them transporting the prey intraorally while they were in the water column. However, when larger cephalopods were handled, we observed morays using the substrate (the bottom of the aquarium) or the side or corner of the aquarium to assist in pushing prey into their mouths. Future investigations using high-speed video are needed to understand whether protraction and retraction distances are different when transporting cephalopods versus fish.

4.3. Distribution of prey manipulation behaviors

Our study revealed that *G. mordax* exhibited a behavioral repertoire similar to that of tropical piscivorous morays, comprised of shaking, knotting, rotating, and ramming when feeding on prey. A PCA provided us with a visual representation of how these behaviors were distributed across trials. Of the four major axes of variation in our data set, PC1 was the only axis that revealed a relationship with RPM for both prey types suggesting that size does have an effect on manipulation duration. PC axes 2–4 revealed some interesting patterns for the distribution of prey manipulation behaviors. Knotting and shaking loaded strongly but in opposite directions along PC2 suggesting that trials where there was predominantly knotting, there was little shaking and vice versa. In trials where knotting accounted for much of the manipulation duration, shaking duration was short or nil. Rotation and ramming, two behaviors that seem to facilitate forcing prey into the gape, loaded negatively on different PC axes revealing that these behaviors could be observed together or separately in a single trial. The PC loadings also suggested that knotting was a behavior commonly observed with rotation or ramming. In a single trial, shaking seemed to be the only behavior that could be observed in combination with any of the other three behaviors, with the exception of knotting. Shaking was also the first behavior employed for smaller prey.

A previous study examining the feeding behavior for three different genera of moray eels discovered that prey size strongly influenced manipulation behaviors (Miller, 1989). In feeding trials with live prey, Miller (1989) noted that two of the three species of morays tended to employ rotation or knotting to manipulate large prey whole or to break large prey into more manageable pieces.

Gymnomuraena zebra, a crab-eating specialist, was the exception, predominantly employing rotational feeding for all prey sizes; the behavior of knotting around prey was absent.

Although our study exhibited behaviors similar to those reported by Miller (1987, 1989), we did not detect a strong influence of RPM on the type of prey manipulation behaviors employed. One possibility for this difference in our results is that we looked at prey size as a continuous trait whereas Miller (1989) assigned categorical variables – “small” and “large” – post hoc. Small prey were those that required minimal manipulation and could be swallowed whole whereas large prey required extensive manipulation in order to be swallowed whole.

4.4. Effects of prey type

Surprisingly, we found that prey type did not significantly influence the behavioral repertoire of the California moray. We had predicted that fish and cephalopods would present different challenges to the predator due to the differences in their mechanical properties. Cephalopods have protein compositions that suggest a low Young's modulus, supporting the idea that they are flexible and less stiff compared to fish. In general, cephalopods are more elastic due to their network of collagen and elastin fibers as well as their circular arrangement of muscles. It has been predicted that resistance to tensile forces would be greatest when force is applied in the direction longitudinal to the long axis of the squid (Kuo et al., 1991). Thompson et al. (2014) showed that circular muscle contractile properties vary transmurally in the mantle of the Atlantic longfin squid, *Doryteuthis pealeii*. The results of Thompson et al. (2014) encourage to think about how different parts of the cephalopods can present different challenges to the predator, especially if the prey are offered live rather than dead and freshly thawed as those used in the present study. In our study, we observed morays pulling on octopus tentacles or squid mantle in the longitudinal direction but also at oblique angles. Whether this was a purposeful feeding strategy needs further investigation as in either scenario, cephalopod prey were consumed whole and took less time to consume compared to fish prey of similar sizes.

Large cephalopods were less often consumed in pieces compared to fish. Overall, our study had more trials with cephalopod prey. If we examine the proportion of prey consumed whole, we find 84% of cephalopods were swallowed whole whereas 55% of fish were swallowed whole. When examining the proportion of total feeding time spent manipulating prey, morays spent more time manipulating fish and less time manipulating cephalopods although total feeding time increased with size for each prey type. We attribute the increase in total feeding time for cephalopods not to an increase in manipulation duration but to the increase in time needed to move the meal into the oral cavity and transport it. Despite differences in RPM and material properties, there was no significant difference in the distribution of manipulation duration when consuming fish or cephalopod prey, even when the effect of prey body size was removed. Thus, swallowing appeared to be a greater challenge than manipulating deceased cephalopod prey. The increase in transport times and the higher rates of transport are interesting and we speculate that, again, this may be attributed to the low Young's modulus of cephalopod prey. We also observed that thawed cephalopod prey was more slippery compared to fish. Therefore, the surface of cephalopod prey may exhibit a lower coefficient of friction, contributing to the longer intraoral transport times without an increase in the number of protraction and retraction events. Without the aid of the substrate to push against, each retraction event may be slower and require more time for the pharyngeal teeth to grip into the prey.

Our experimental design consisted of feeding wild-caught morays freshly thawed prey for which we could easily manipulate

RPM and IR. Feeding morays thawed prey enabled us to understand how two different prey types (fish and cephalopods) of varying size combinations (mass and diameter) affect manipulation behavior and total feeding time. Replicating our study with live prey would presumably lead to different conclusions. For example, total feeding times would likely be much higher across all prey sizes and might reflect the prowess of both predator and prey. We also predict that there would be a weaker relationship between prey size and total feeding time than what we observed in the current study. Also, the relationship between prey size and prey manipulation duration may be steeper if larger prey are more aggressive than smaller prey. Alternatively, it is also conceivable that small evasive prey could potentially be more challenging to grip and might therefore present more of a challenge in terms of manipulation. Therefore, we recognize that live prey items have the potential to change the outcome of our experiments. Examining the effects of live prey will be the next step in this study, with a proper experimental set-up to accommodate evasive tactics of both the prey and the predator.

4.5. Maximum prey size

We used two different metrics (IR and RPM) to describe prey size in relation to the predator. While cephalopods never exceeded 30% of the mass of a moray and fish never exceeded 20% of moray mass, IRs in both prey categories exceeded maximum horizontal gape distance, yielding IRs > 1. We can attribute the fact that squid having a larger maximum RPM were consumed whole to their tensile properties, therefore being less likely to break apart. Larger fish prey elicited behaviors such as knotting which resulted in small pieces being torn from these prey, thus ceasing the trial. Morays more frequently consumed cephalopods whole and more time was spent swallowing cephalopod prey rather than manipulating it.

While a handful of studies have reported prey items from the stomachs of tropical morays, none of these report predator–prey size relationships for single prey items as a proportion of predator body weight. Young and Winn (2003) studied the diet of two tropical moray species, *Gymnothorax moringa* and *Gymnothorax vicinus*, and reported that individuals of both species were found to have up to four individual wrasses (*Halichoeres* sp.) in their stomachs. This study also reported RPM from an observation where an individual *G. vicinus* regurgitated a squirrel fish (*Holocentrus ascensionis*) that was 14% of its body mass. This observation coincides with the maximum RPM for fish in our laboratory study. Our own field observations also support our controlled laboratory study of moray feeding performance as we have manually palpated a kelp bass (RPM: 13%) from the stomach of a moray.

4.6. Conclusions

In the wild, moray eels consume a wide variety of vertebrate and invertebrate prey of various sizes. In our present study, size of prey, rather than type, significantly influenced the total feeding time and manipulation behaviors employed by the California moray. While total manipulation duration was responsible for the increase in total feeding time for fish prey, intra-oral transport time drove longer total feeding times for cephalopod prey. Knotting, shaking, rotational feeding, and ramming were prey manipulation behaviors observed in *G. mordax*. While the durations of each of these behaviors increased with prey size, the distribution of manipulation behaviors was not influenced by prey type. Maximum prey size, measured in RPM, differed between fish (0.14) and cephalopods (0.27). Maximum prey size for fish in our laboratory study corresponded to field observations around Catalina Island and those reported for tropical moray species. Despite the perceived difficulty swallowing cephalopods, the range of relative prey mass and

therefore, maximum prey size swallowed whole was greater for cephalopods than fish.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.zool.2017.03.002>.

References

- Arrington, D.A., Winemiller, K.O., Loftus, W.F., Akin, S., 2002. How often do fishes run on empty? *Ecology* 83, 2145–2151.
- Barley, S.C., Mehta, R.S., Meeuwij, J.J., Meekan, M.G., 2015. To knot or not? Novel feeding behaviours in moray eels. *Mar. Biodivers.* 46, 703–705.
- Bone, Q., Pulsford, A., Chubb, A.D., 1981. Squid mantle muscle. *J. Mar. Biol. Assoc. UK* 61, 327–342.
- Chave, E.H., Randall, H.A., 1971. Feeding behavior of the moray eel *Gymnothorax pictus*. *Copeia* 1971, 570–574.
- Cruz-Neto, A.P., Andrade, D.V., Abe, A.S., 2001. Energetic and physiological correlates of prey handling and ingestion in lizards and snakes. *Comp. Biochem. Physiol. A* 128, 513–531.
- Cundall, D., Deufel, A., 2006. Influence of the venom delivery system on intraoral prey transport in snakes. *Zool. Anz.* 245, 193–210.
- Cundall, D., Greene, H.W., 2000. Feeding in snakes. In: Schwenk, K. (Ed.), *Feeding: Form, Function, and Evolution in Tetrapod Vertebrates*. Academic Press, San Diego, pp. 293–333.
- de Queiroz, A., 1984. Effects of prey type on the prey handling behavior of the bull snake, *Pituophis melanoleucus*. *J. Herpetol.* 18, 333–336.
- de Queiroz, A., de Queiroz, K., 1987. Prey-handling behavior of *Eumeces gilberti* with comments on head first ingestion in squamates. *J. Herpetol.* 21, 57–63.
- Dill, L.M., Fraser, A.H.G., 1984. Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). *Behav. Ecol. Sociobiol.* 16, 65–71.
- Eschmeyer, W.N., Herald, E.S., Hammon, H., 1983. *A Field Guide to Pacific Coast Fishes of North America*. Houghton Mifflin Co., Boston.
- Gillen, A.L., Stein, R.A., Carline, R.F., 1981. Predation by pellet-reared tiger muskellunge on minnows and bluegills in experimental systems. *Trans. Am. Fish Soc.* 110, 197–209.
- Greene, H.W., 1983. Dietary correlates of the origin and radiation of snakes. *Am. Zool.* 23, 431–441.
- Grubich, J.R., Rice, A.N., Westneat, M.W., 2008. Functional morphology of bite mechanics in the great barracuda (*Sphyrna barracuda*). *Zoology* 111, 16–29.
- Harper, D.G., Blake, R.W., 1988. Energetics of piscivorous predator–prey interactions. *J. Theor. Biol.* 134, 59–76.
- Harrison, J.S., Higgins, B.A., Mehta, R.S., 2017. Scaling of dentition and prey size in the California moray, *Gymnothorax mordax*. *Zoology* 120.
- Helfman, G.S., Clark, J.B., 1986. Rotational feeding: overcoming gape-limited foraging in anguillid eels. *Copeia* 1986, 679–685.
- Hiatt, R.W., Strasburg, D.W., 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Monogr.* 30, 65–127.
- Huey, R.B., Pianka, E.R., Vitt, L.J., 2001. How often do lizards run on empty? *Ecology* 82, 1–7.
- Jayne, B.C., Voris, H.K., Ng, P.K.L., 2002. Snake circumvents constraints on prey size. *Nature* 418, 143.
- Jolicoeur, P., 1963. The multivariate generalization of the allometry equation. *Biometrics* 19, 497–499.
- Kaspari, M., 1990. Prey preparation and the determinants of handling time. *Anim. Behav.* 40, 118–126.
- Kuo, J.D., Hultin, H.O., Atallah, A.T., Pan, B.S., 1991. Role of collagen and contractile elements in ultimate tensile strength of squid mantle. *J. Agri. Food Chem.* 39, 1149–1154.
- Liem, K.F., 1979. Modulatory multiplicity in the feeding mechanism in cichlid fishes, as exemplified by the invertebrate pickers of Lake Tanganyika. *J. Zool.* 189, 93–125.
- Loop, M.S., Bailey, L.G., 1972. The effects of prey size on the ingestion behavior of rodent-eating snakes. *Psychon. Sci.* 28, 168–169.
- MacNulty, D.R., Tallian, A., Stahler, D.R., Smith, D.W., 2014. Influence of group size on the success of wolves hunting bison. *PLoS One* 9, e112884.

- McCleneghan, K., 1973. The ecology and behavior of the California moray eel *Gymnothorax mordax* (Ayres 1958) with description of its larva and the leptocephali of some other East Pacific Muraenidae. Ph.D. Thesis. University of Southern California, Los Angeles.
- Mehta, R.S., Burghardt, G.M., 2008. Contextual flexibility: reassessing the effects of prey size and status on prey restraint behaviour of macrostomate snakes. *Ethology* 114, 133–145.
- Mehta, R.S., Wainwright, P.C., 2007. Raptorial jaws in the throat help moray eels swallow large prey. *Nature* 449, 79–82.
- Mehta, R.S., Wainwright, P.C., 2008. Functional morphology of the pharyngeal jaw apparatus in moray eels. *J. Morphol.* 269, 604–619.
- Miller, T., 1987. Knotting: a previously undescribed feeding behavior in muraenid eels. *Copeia* 1987, 1055–1057.
- Miller, T., 1989. Feeding behavior of *Echidna nebulosa*, *Enchelycore pardalis*, and *Gymnomuraena zebra* (Teleostei: Muraenidae). *Copeia* 1989, 662–672.
- Nakazawa, T., Shin-ya, O., Masayuki, U., 2013. Predator–prey body size relationships when predators can consume prey larger than themselves. *Biol Letters* 9, 20121193.
- Page, H., Brooks, A., Kulbicki, M., Galzin, R., 2013. Stable isotopes reveal trophic relationships and diet of consumers in temperate kelp forest and coral reef ecosystems. *Oceanography* 26, 180–189.
- Pough, F.H., Groves, J.D., 1983. Specializations of the body form and food habits of snakes. *Am. Zool.* 23, 443–454.
- R Development Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria <http://www.R-project.org/>.
- Reece, J.S., Mehta, R.S., 2013. Evolutionary history of elongation and maximum body length in moray eels (Anguilliformes: Muraenidae). *Biol. J. Linn. Soc.* 109, 861–875.
- Scharf, F.S., Juanes, F., Rountree, R.A., 2000. Predator size–prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Mar. Ecol. Prog. Ser.* 208, 229–248.
- Shine, R., Thomas, J., 2005. Do lizards and snakes really differ in their ability to take large prey? A study of relative prey mass and feeding tactics in lizards. *Oecologia* 144, 492–498.
- Shurin, J.B., Gruner, D.S., Hillebrand, H., 2006. All wet or dried up? Real differences between aquatic and terrestrial food webs. *Proc. R. Soc. London B* 273, 1–9.
- Thompson, J.T., Shelton, R.M., Kier, W.M., 2014. The length–force behavior and operating length range of squid muscle vary as a function of position in the mantle wall. *J. Exp. Biol.* 217, 2181–2192.
- Warton, D.I., Wright, I.J., Falster, D.S., Westoby, M., 2006. A review of bivariate line-fitting methods for allometry. *Biol. Rev.* 81, 259–291.
- Werner, E.E., Hall, D.J., 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55, 1042–1052.
- Young, R.F., Winn, H.E., 2003. Activity patterns, diet, and shelter site use for two species of moray eels, *Gymnothorax moringa* and *Gymnothorax vicinus*, in Belize. *Copeia* 2003, 44–55.
- Yukihira, H., Shibuno, T., Hashimoto, H., Gushima, K., 1994. Feeding habits of moray eels (Pisces: Muraenidae) at Kuchierabu-jima. *Appl. Biol. Sci.* 33, 159–166.